Diet Quality Differentially Affects Breeding Effort of *Mastomys coucha* and *M. natalensis*: Implications for Rodent Pests

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ABSTRACT   In this study we compare the reproductive ability of *Mastomys natalensis*, an agricultural rodent pest and that of the closely related species *M. coucha*, which has not been ascribed as a pest. We suggest that the ability of *M. natalensis* to plague, as well as dominate, resource-limited habitats, may in part be related to its differential breeding response to variation in diet quality. Thus, we examined the reproductive response of *M. coucha* and *M. natalensis* mothers to variation in dietary protein intake. Our results demonstrated that typical levels of reproduction extended over a narrower range of dietary protein content for *M. coucha* than *M. natalensis* females. Only *M. natalensis* females bred on 6% protein diets, while on 20% protein diets the reproductive output of *M. coucha* was lower than on diets containing 10– and 15% protein. *M. natalensis* responded to low protein diets by reducing litter size and litter mass but not individual pup mass. Thus, providing diet quality improves before parturition, conception under sub-optimal conditions may not compromise individual pup growth. Furthermore, the ability of *M. natalensis* to breed under conditions of low diet quality may advance their breeding season compared to species that cannot breed until diet quality improves, allowing *M. natalensis* to produce additional litters through the season, while more daughters could reproduce during the season of their birth, both factors that are known to contribute to the plaguing tendency of *M. natalensis*. *J. Exp. Zool. 301A:97–108, 2004.*   © 2004 Wiley-Liss, Inc.

INTRODUCTION

Many studies of rodent spatiotemporal population dynamics indicate the importance of either density dependent (e.g. Tkadlec and Zejda, '98; Hansen et al. '99; Saitoh et al., '99) or density-independent factors in shaping populations. However, present syntheses of spatiotemporal rodent population dynamics suggest that, for a number of species, their dynamics can be related to both stochastic environmental factors and deterministic density-dependent factors (Leirs et al., '97; Lewellen and Vessey, '98 a,b; Lima et al., '99; Karels and Boonstra, 2000). In doing so these studies have integrated the available data suggesting the importance of both stochastic and density dependent models to rodent population dynamics. This integrated approach has provided important insights into temporal differences between these factors. For rodents that exhibit sporadic outbreaks Leirs et al. ('96) and others emphasise the positive relationship of outbreaks to exogenous forces, followed by a delayed non-linear effect of population density. Thus, stochastic environmental factors such as rainfall, that act on food quality and quantity, are of fundamental importance in triggering outbreaks.

For populations that reach pest, or plague proportions, both the onset of the breeding period and female natality rates are crucial in determining future plague events. Rodent plagues are typically related to an early onset of the breeding season (Singleton et al., 2001), associated with early rainfall (Leirs et al., '96) and leading in turn to greater seasonal recruitment. Early rain is important in allowing females to produce additional litters within the season (Ims, '87), presumably as a result of an earlier increase in diet quality through the year. In addition the progeny of early-breeding females may themselves reproduce later in the same season (Leirs et al., '93), rather than having to delay breeding until the

next season. Population models have repeatedly indicated that pest species with high turnover rates (high reproduction, high mortality, short generation times) are more sensitive to reductions in fecundity than increases in mortality rates (Krebs, '99; Stenseth et al., 2001). Thus, the ability of rodent pests to maximise population growth should be related to maximising recruitment through early and sustained breeding. Consequently any mechanisms allowing an earlier onset of breeding, or increasing natality rates, should augment a species' ability to plague.

Diet quality and not quantity is considered one of the most important factors regulating the onset of rodent breeding (Bomford, '87a), including *M. natalensis* (Leirs et al., '90). Arguably the most important contributing factor is dietary protein, through its effect on female breeding parameters (Hoffmann, '58; Bomford, '87b). Artificial food supplementation experiments have been widely employed to examine the effect of food supply on population dynamics (reviewed by Boutin, '90). However, while many ecologists have manipulated food quantity, food quality has only been considered in a handful of studies (see Boutin, '90). Furthermore, the majority of studies have considered the effects of food quality on a single species, rather than addressing interspecific differences in species' responses to diet quality. However, a food supplementation study by Krebs and DeLong ('65) in an area inhabited by California voles *Microtus montanus* and house mice *Mus musculus* showed that a slight increase in the vole population was followed by a steady decline. At the same time the house mouse population underwent a five-fold increase for which the peak density coincided with the initial decline in vole density (DeLong, '67). Conversely, Ford and Pitelka ('84) demonstrated that, in the absence of mice, supplementation led to greater vole numbers. The implication is that high mouse density inhibited vole population growth. Thus differential responses to food supply, possibly through differential reproduction, may also be important in interspecific interactions.

In the present study we examine the breeding effort of two species of multi-mammate mice, *M. natalensis* and *M. coucha*, in relation to differences in diet quality. Whereas *M. natalensis* is known as a serious pest species in sub-Saharan Africa, due to its ability to undergo major population outbreaks, no similar outbreaks have been ascribed to *M. coucha*. Furthermore *M. natalensis* is known to dominate rodent communities in recently dis-

turbed habitats, which may be resource limited. In this study we examine the reproductive parameters of female multi-mammate mice in relation to diet quality. We hypothesise that *M. natalensis* should show an increased reproductive effort relative to *M. coucha*, conforming to a rodent capable of reaching plague proportions. We also predict that *M. natalensis* should be able to maintain greater reproductive effort on poorer quality diets than *M. coucha*, thus demonstrating interspecific differences in these species to exploit resource-limited habitats.

MATERIALS AND METHODS

Multimammate mouse life history

Two species of mulitmammate mice, *Mastomys coucha* and *M. natalensis*, occur in southern Africa (Granjon et al., '97). *Mastomys coucha* is endemic to the region, while *M. natalensis* is widespread through sub-Saharan Africa. The two species cannot be distinguished morphologically in the field and identification is dependent on cytogenetic markers (Green et al., '78; Granjon et al., '97; Smit et al., 2001) or multivariate discriminant analyses of skull measurements (Dippenaar et al., '93). Rainfall may be an important determinant of their distribution patterns as *M. natalensis* generally occur in areas with >600mm annual rainfall and *M. coucha* in drier areas, with an annual precipitation of <700mm (Gordon, '84), the two species occurring sympatrically within the 600–700mm rainfall isohyets. These data suggest that *M. natalensis* may not be able to tolerate the less mesic areas of the region. However, the absence of *M. coucha* from the wetter areas is unclear, though a likely explanation would be interspecific competition giving rise to differences in the habitat preferences of these closely related species.

Mastomys natalensis is the most common murid rodent of sub-Saharan Africa (Fiedler, '88a). Due to its sporadic population outbreaks it is considered an agricultural pest (Fiedler, '88b). The breeding potential of this species, together with its high turnover rate (Leirs et al., '96) allows it to dominate within disturbed habitats affected by factors including fire (Meester et al., '79; Swanepoel, '81), drought, overgrazing (Bowland and Perrin, '88), or mining (Chidumayo, '80; Ferreira and van Aarde, '96). It is also dominant on fallow agricultural ground (Christensen, '96).

Breeding is strictly seasonal and is linked to the seasonality of rainfall (e.g. Swanepoel, '80; Chidumayo, '84; Leirs et al., '90). While *M. natalensis*

may use germinating grass as an environmental predictor (Leirs et al., '94; Firquet et al., '96), the maintenance of breeding behaviour is more likely related to diet quality. Seasonal differences in the diet of *M. natalensis* indicate an increase in the proportion of insects/protein and a decrease in carbohydrates/plant material through the breeding season (Monadjem, '98). Thus, Field ('75) suggested their diet did not contain sufficient protein during the dry season to maintain reproduction and also that water stress could impair protein metabolism. However, in areas receiving artificial irrigation, such as agricultural areas, breeding may extend through the year (Swanepoel, '80; Firquet et al., '96), while reproduction around domiciles continues during periods of reproductive cessation in surrounding agricultural land (Chidumayo, '84; Leirs, unpublished observations). Food limitation has been suggested as the mechanism curtailing reproductive activity (Christensen, '93), and while food supplementation (quantity) studies have extended the breeding period (Monadjem and Perrin, '96), they have not prevented a break in reproduction (Leirs et al., '90), advanced the onset of breeding (Monadjem and Perrin, '96), or induced reproductive activity during non-breeding periods (Taylor and Green, '76).

Despite the extensive data available for *M. natalensis*, few ecological data are available that positively identify *M. coucha*. This may partly be due to the difficulties in positively identifying the two species and it is highly likely that some studies in southern Africa, supposedly examining *M. natalensis*, may in fact have been conducted on *M. coucha*. However, *M. coucha* is known to occur through a wide variety of habitats within its distributional range (Avenant, '97), where it may dominate rodent communities (Avenant, 2000).

Animal maintenance

All experiments were conducted under controlled laboratory conditions (25°C, 14L:10D) at the University of Pretoria, South Africa. The ethical committee of the Faculty of Biological and Agricultural Sciences of the University sanctioned all holding and handling procedures. Thirty captive breeding pairs of *M. natalensis* were established from individuals captured at Richards Bay (28°43'S, 32°12'E), KwaZulu/Natal, while 30 pairs of *M. coucha* were established using animals captured at Pretoria (25°45'S, 28°14'E), Gauteng. The species status of individuals was confirmed by

gel electrophoresis (G. Campbell, pers. comm.). Commercial mouse pellets (Epol Animal Feed Manufacturers, P.O. Box 19096, Pretoria West, South Africa) and water were provided *ad libitum*. In addition animals were provided with fresh sawdust bedding and plastic shelters.

Litters produced by these wild-caught pairs were removed at weaning age (21 days, Meester, '60), and fed mouse pellets ad libitum until 50 days old. As the earliest recorded first oestrus cycle for *Mastomys* is recorded as 54 days (Meester, '60) these offspring were then randomly paired (not with siblings) and assigned to one of four treatment groups (6, 10, 15, or 20% protein diets) at the age of 50 days, following the protocol of Lamb and van Aarde (2001). Twenty breeding pairs were established for both species on each treatment group. A protein content of 6% was not considered unrealistically low in our laboratory protocol, as dietary protein levels of 4–8% (Bomford and Redhead, '87; Cameron and Eshelman, '96) have been recorded in rodent field studies.

The experimental diets (Animal Nutrition and Animal Products Institute, Private Bag X2, Irene, 0062, South Africa) were designed so that all nutritional components, except digestible protein content, which varied according to treatment level, remained constant (Lamb and van Aarde, 2001; Table 1). Animals received 10g per day of treatments containing an optimal digestible protein content of 6–, 10–, 15–, or 20%. Digestible energy content remained constant at approximately 123 kJ; sufficient energy for growth and reproduction (Perrin and Clarke, '87).

Females, as well as their pups, were weighed at *partum* (Ohaus Precision Advanced Balance, Ohaus Corporation, New Jersey, USA) and an index of maternal reproductive effort was calculated as [litter mass/maternal mass], while additional data were collected on litter sex ratio, litter size, and litter mass. Only data from multiparous females were used and the second to fourth litters were kept with their parents until weaning at 21 days. Only two males and two females from each litter were left with the breeding pair to be raised, in order to control for the possible effect of litter size on pup growth rates from birth to weaning. Weaning weights of individual pups were also recorded, as was the percentage of pups surviving from birth to weaning. As breeding pairs were not separated through the experimental period, interlitter intervals were also calculated from the dates of successive litters for each experimental pair. Given a gestation period of 23 days (Johnston and

TABLE 1. *Composition and nutritional content of 6% protein diet used in Mastomys feeding trials. For composition of 10-, 15- and 20% protein diets see Lamb and van Aarde (2001)*

Ingredients	Formulated (%)	Formulated (mass)	Nutritional Content	
Fine Bran	4.4	44	Crude Fibre (%)	5
Corn Starch	45.8	458	Fat (%)	1.75
Alfalfa Meal 15%	14.6	146	Crude Protein (%)	5.7
L-Lysine Hcl	0.2	2	Lysine (%)	0.33
Vitamin & Mineral Premix	0.5	5	Methionine+Cystine (%)	0.18
Limestone	0.5	5	Threonine (%)	0.2
Monocalcium Phosphate	7.3	73	Calcium (%)	1.65
Salt	0.8	8	Phosphorous (%)	2
Maize	26.0	260	Digestible energy (kJ/g)	12.3

Oliff, '54) the date of sexual maturity was calculated as 23 days prior to that of parturition.

Data were grouped into a two-way ANOVA designed to examine the effects of species and dietary protein on female reproductive, litter, and individual offspring parameters. Preliminary analyses indicated no significant differences in maternal or offspring parameters for successive litters. Consequently litter order effects could be excluded from analyses and mean values were used for each female and her pups for all parameters except age of sexual maturity. Analyses were conducted using the *Statistica* software package (Statsoft, Inc., '96). In cases for which an interaction existed between variables (species and diet), Tukey-tests were conducted on the subgroups for each species, following Sokal and Rohlf ('95, p. 336) in order to determine the statistical nature of such interactions.

RESULTS

Female reproductive parameters

Only *M. natalensis* females bred on 6% protein diets, whereas both species bred on the 10, 15, and 20% protein diets. Thus interspecific data could only be compared for 10–20% protein diets, while additional intraspecific comparisons of the effect of diet on breeding variables on *M. natalensis* are presented for 6% protein diets.

Maternal mass

Maternal post partum body mass did not differ significantly between the two species, though females on the 20% protein diet were significantly heavier post partum than females on 10–15% protein diets (Table 2). The body mass of *M. natalensis* on a 6% diet (43.4 ± 1.5g, n=16) did

not differ significantly with that of females on alternative diets (Fig. 1a).

Sexual maturity

The earliest recorded age of sexual maturity was 54 days for *M. natalensis* (on 20% dietary protein) and 45 days for *M. coucha* (on 10% dietary protein). Age of sexual maturity was significantly different for both diet and species, with an interaction between diet and species (Table 2). Thus, female *M. coucha* on 20% diets reached sexual maturity at a much older age than on 10–15% diets, whilst age of sexual maturity for *M. natalensis* was greater on 15% than either 10– or 20% diets (Table 2). The age of sexual maturity of *M. natalensis* on the 6% protein diet (148.8 ± 6.6 days, n=18) did not differ significantly with that of females on 15% protein diets, but did with those on 10– and 20% protein diets (Fig. 1b).

Inter-litter interval

Minimum recorded inter-litter periods were 20 days for *M. natalensis* (on 20% dietary protein) and 23 days for *M. coucha* (on 10% dietary protein). Inter-litter intervals did not differ significantly when considering species or diet separately, though there was a significant interaction between species and diet (Table 2). Thus, while inter-litter interval was greater for *M. coucha* on a 20% protein than other diets, it was greater for *M. natalensis* fed a 15% protein diet than on alternative diets. Furthermore, the inter-litter interval of *M. natalensis* females on a 6% protein diet (42.1 ± 2.7 days, n=18) did not differ significantly with that of females on any other diet (Fig. 1c). For both species there was an apparent relationship between age of sexual maturity and

TABLE 2. *Comparative female reproductive characteristics for Mastomys coucha and M. natalensis females maintained on diets containing different percentages of dietary protein, but of equal energetic values. Results for trials expressed as mean ± SE. Results of two-way ANOVAs include probability (*P < 0.05; **P < 0.02; ***P < 0.001) and F values. The relative direction of any interaction between (diet) and (species) are discussed in the text*

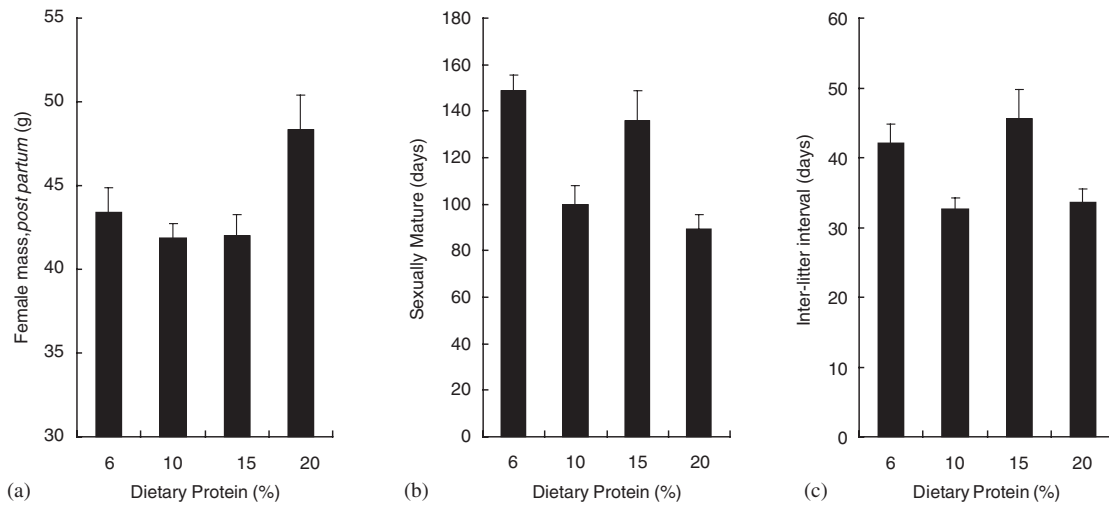|	M. coucha			M. natalensis			Effects		
	10%	15%	20%	10%	15%	20%	Spp.	Diet	Spp. x Diet
Female mass *post partum* (g)	44.5±1.3	45.4±1.9	47.9±1.7	41.8±0.9	42.0±1.3	48.3±2.1	2.04	5.64***	0.82
Sexually mature (days)	92.6±7.8	116.3±16.0	192.1±21.5	99.9±8.0	135.9±12.7	89.4±5.9	5.63**	6.03***	13.33***
Inter-litter Interval (days)	34.5±2.4	34.7±4.7	43.0±4.7	32.7±1.6	45.7±4.1	33.7±1.9	0.00	1.93	4.45**
n	(19)	(18)	(16)	(16)	(18)	(19)			

Fig. 1. The effect of dietary protein intake on female *Mastomys natalensis* reproductive parameters including (a) female *post partum* mass; (b) age of sexual maturity and (c) inter-litter interval.

inter-litter interval with those females (15% *M. natalensis* and 20% *M. coucha*) maturing later also exhibiting greater inter-litter intervals.

Litter parameters

Litter size

The number of pups in *M. coucha* litters was significantly greater than those in *M. natalensis* litters (Table 3), though diet did not influence litter size for either species on 10–20% protein diets. However, when 6% protein diets were also considered for *M. natalensis*, these litters (6.0±0.3, n=17) were significantly smaller than those produced by females on either 15– or 20% diets, but not from those of females on a 10% protein diet (Fig. 2a).

Interspecific differences in litter sizes were related to the number of male pups in litters, which were greater in *M. coucha* than *M. natalensis* litters (Table 3), whereas the number of female pups did not differ significantly between litters (Table 3). When the 6% diet was also considered, the number of *M. natalensis* males born on this diet (3.0±0.2, n=17) was significantly lower than on the 15– or 20% protein diets (Fig. 3), though female numbers (2.9±0.2, n=17; Fig 3) did not differ significantly with treatment.

There were, however, no significant differences in the sex ratios of litters (Table 3), possibly due to the relatively small differences in male numbers. When compared to the number of male pups expected for parity (*i.e.* a sex ratio of 1:1), the observed number of male pups in litters did not

TABLE 3. *Comparative characteristics of litters produced by Mastomys coucha and M. natalensis females maintained on diets containing different percentages of dietary protein, but of equal energetic values. Results for trials expressed as mean ± SE. Results of two-way ANOVAs include probability (*P < 0.05; **P < 0.02; ***P < 0.001) and F values*

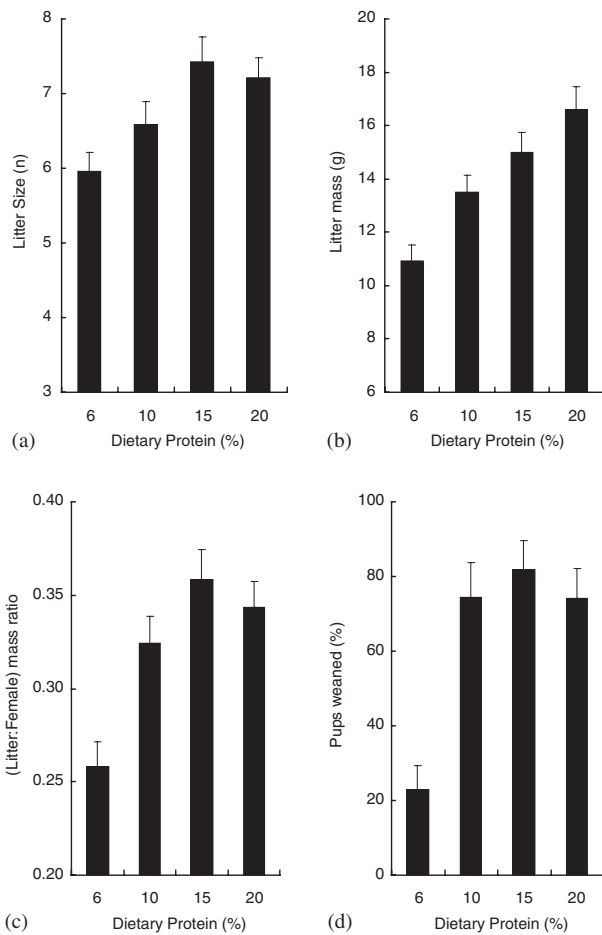|	M. coucha			M. natalensis			Effects		
	10%	15%	20%	10%	15%	20%	Species	Diet	Spp. x Diet
Litter size (n)	7.6±0.4	8.1±0.4	7.7±0.5	6.6±0.3	7.4±0.3	7.2±0.3	5.44**	1.56	0.27
Male pups (n)	4.0±0.3	3.9±0.3	4.4±0.3	3.3±0.2	3.8±0.2	3.8±0.2	4.96*	1.56	0.79
Female pups (n)	3.6±0.3	4.2±0.3	3.3±0.3	3.3±0.2	3.6±0.3	3.5±0.2	0.57	2.05	0.36
Litter sex ratio(m:f)	0.53±0.03	0.48±0.03	0.58±0.02	0.50±0.02	0.51±0.03	0.52±0.02	1.14	2.30	1.77
Litter mass (g)	15.4±0.9	17.7±1.2	17.9±1.4	10.9±0.6	13.5±0.7	15.0±0.9	6.03**	4.42**	0.78
Pups weaned (%)	52.2±9.6	61.6±9.6	68.1±8.1	74.5±9.2	81.9±7.7	74.1±7.9	5.04*	0.57	0.49
Litter mass/maternal mass	0.34±0.01	0.40±0.02	0.37±0.02	0.32±0.01	0.36±0.02	0.34±0.01	4.40*	3.66**	0.26
n	(18)	(16)	(16)	(16)	(18)	(19)			

Fig. 2. The effect of female dietary protein intake on *Mastomys natalensis* litter parameters including (a) litter size; (b) litter mass; (c) litter:female mass ratio and (d) percentage of pups weaned.

differ significantly for any treatment (*G* test; *M. natalensis*: 5% diet, $G=4.81$, df=16, NS; 10% diet, $G=4.16$, df=15, NS; 15% diet, $G=11.09$, df=17,
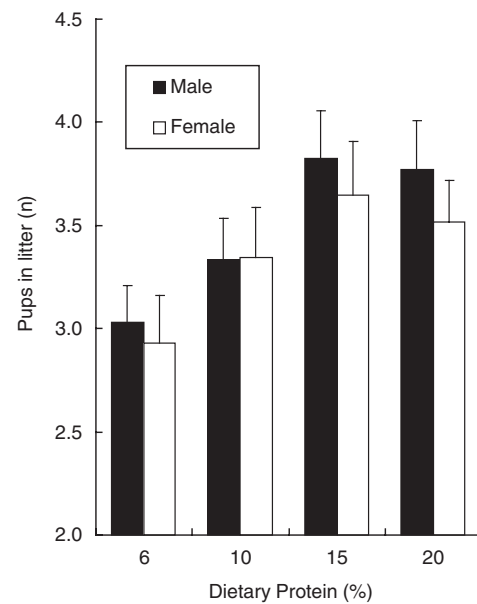

Fig. 3. The effect of female dietary protein intake on the average size of *Mastomys natalensis* litters.

NS; 20% diet, $G=17.68$, df=18, NS; *M. coucha*: 10% diet, $G=18.67$, df=18, NS; 15% diet, $G=-6.14$, df=15, NS) except female *M. coucha* on a 20% protein diet, which produced significantly more male pups than expected (*G* test: $G=46.04$, df=15, p<0.001).

Litter mass

Mass of *M. coucha* litters was significantly heavier than that of *M. natalensis* litters, while litters produced by mothers of both species on 10% diets were significantly lighter than those of mothers on 20% diets (Table 3). Litter mass of females on 15% diets did not differ significantly

with that of 10– or 20% diets. For *M. natalensis* on a 6% protein diet, litter mass (10.93 ± 0.60g, n=16) was significantly less than that of females on 15– and 20% diets, but not on 10% diets, indicating a decrease in litter mass with a decrease in diet quality (Fig. 2b).

Litter:maternal mass

Female reproductive effort, measured as (litter mass:female mass) indicated that females on 10% protein diets produced relatively lighter litters in relation to their own post partum body mass than those on 15– and 20% diets (Table 3). Furthermore, the reproductive effort (litter mass: maternal mass) of *M. coucha* females was greater than that of *M. natalensis* females (Table 3). The litter mass: maternal mass of *M. natalensis* mothers on 6% dietary protein (0.26 ± 0.01, n=16) was significantly lower than that of females on alternative diets (Fig. 2c).

Pups weaned

Despite the apparently larger, heavier litters of *M. coucha* compared to *M. natalensis*, their reproductive output was compromised by the percentage of pups weaned at 21 days, which was significantly lower than for *M. natalensis* females (Table 3). For 10–20% protein diets there was no effect of diet on pup mass at weaning, though the percentage of pups weaned by *M. natalensis* females on the 6% diet (22.9 ± 6.5%, n=18) was substantially lower than for other dietary regimes (Fig. 2d).

Pup parameters

For both *Mastomys* species, male and female birth weight was influenced by diet (Table 4), mothers giving birth to relatively heavier offspring, both sons and daughters, on the 20% rather than on 10– or 15% diets. Furthermore, within each class of dietary protein, no significant differences were found between male and female birth weights for either species (ANOVA; *M. natalensis*: $F_{1,136}=1.95$, NS; *M. coucha*: $F_{1,96}=1.47$, NS). There was no significant difference in pup mass of male (1.93 ± 0.06g, n=16; Fig. 4a) or female (1.92 ± 0.08g, n=16; Fig 4a) *M. natalensis* on 6% diets compared to 10– or 15% diets, though these pups were lighter than those born to females on a 20% protein diet.

However, by time of weaning significant interspecific differences had developed in the body mass of both male and female pups (Table 4), which was also dependent of diet. Thus, the weaned weight of male *M. coucha* was greater than that of *M. natalensis*. There was also an interaction between diet and species. For *M. coucha*, male pups on 15– and 20% diets did not differ significantly in weight, while those on a 10% diet were significantly lighter than other pups. The same pattern was true for female pups. The weaned mass of 10–and 20% male *M. natalensis* pups differed significantly, while that of 15% male pups was intermediate, not differing from 10– or 20% pups. In addition male pups of females fed a 6% protein diet were significantly lighter ($7.35 \pm g0.40$g; Fig. 4b) at weaning than those on any other diet. This pattern varied slightly for female pups, for which there was again a significant difference in the weight of pups on 10– and 20% diets. However, female pups on a 15% diet were significantly lighter than those weaned from mothers on a 20% diet, though their weights did not differ significantly with pups on a 10% diet. Females from 6% protein mothers reached substantially lighter mass at weaning than female pups on other diets (7.04 ± 0.32g; Fig. 4b). There were no sex-specific differences in the weaning mass of pups on any diet (ANOVA; *M. natalensis*: $F_{1,107}=0.73$, NS; *M. coucha*: $F_{1,86}=1.11$, NS). Thus pups did not exhibit sexual body mass dimorphism at either birth or weaning.

DISCUSSION

Our results clearly demonstrate that, under conditions of intermediate food quality, *M. natalensis* and *M. coucha* females breed at similar rates. However, at more extreme levels of diet quality, their reproductive abilities differ. The most striking aspect is the ability of *M. natalensis* to continue breeding at levels of dietary protein intake insufficient to maintain reproductive activity in *M. coucha*. The continued breeding activity of *M. natalensis* is presumably related to its ability to move into and rapidly colonise disturbed habitats (Meester et al., '79; Swanepoel, '81; Ferreira and van Aarde, '96), for which food quality may be low. This should certainly be true for the quality of food material following burning, mining operations, or ploughing for which plant cover and also invertebrate biomass would be reduced. Such reproductive flexibility would allow *M. natalensis* to monopolise habitats providing inadequate nutritional conditions for species such as *M. coucha* to reproduce successfully, allowing a consequent increase in population numbers.
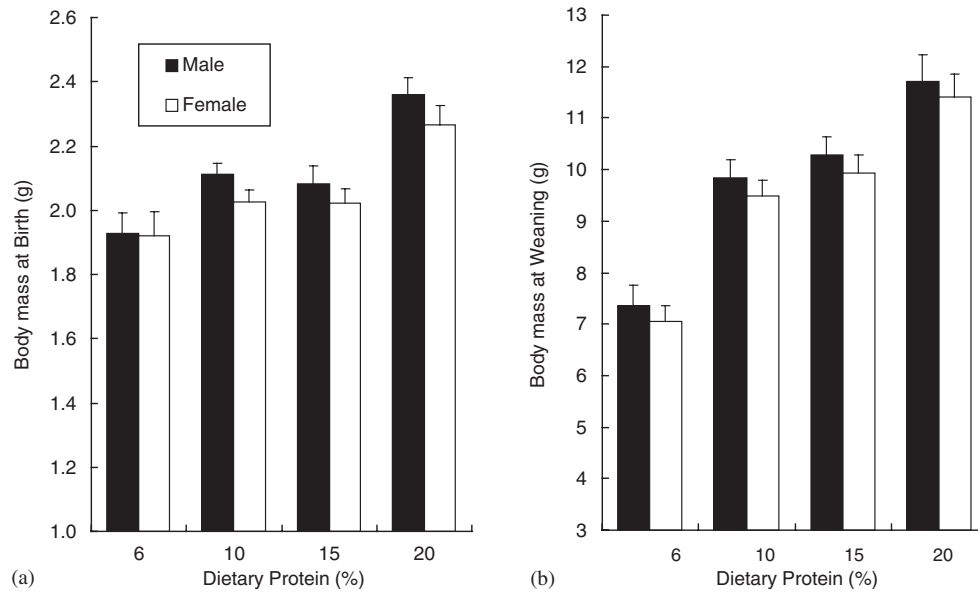
Fig. 4. The effect of female dietary protein intake on the average body mass of *Mastomys natalensis* pups at birth (age 0 days) and weaning (age 21 days).

TABLE 4. *Comparative characteristics of individual pups produced by Mastomys coucha and M. natalensis females maintained on diets containing different percentages of dietary protein, but of equal energetic values. Results for trials expressed as mean $\pm$ SE. Results of two-way ANOVAs include probability (*P√0.05; **P√0.02; ***P√0.001) and F values. The relative direction of any interaction between (diet) and (species) are discussed in the text*

	M. coucha			*M. natalensis*			*Effects*		
	10%	15%	20%	10%	15%	20%	Spp.	Diet	Spp. x Diet
Birth									
Female, birth (g)	2.00 ± 0.21	2.17 ± 0.05	2.24 ± 0.06	2.02 ± 0.04	2.02 ± 0.05	2.27 ± 0.06	0.64	11.35***	2.04
Male, birth (g)	2.06 ± 0.05	2.23 ± 0.05	2.30 ± 0.06	2.11 ± 0.03	2.08 ± 0.06	2.36 ± 0.05	0.06	11.76***	2.58
(n)	(17)	(16)	(16)	(16)	(18)	(19)			
Weaning									
Female, weaning (g)	9.87 ± 0.46	12.04 ± 0.35	11.30 ± 0.38	9.49 ± 0.29	9.93 ± 0.36	11.40 ± 0.46	5.99**	9.70***	4.27**
Male, weaning (g)	10.04 ± 0.53	12.58 ± 1.35	11.87 ± 0.45	9.84 ± 0.34	10.28 ± 0.35	11.72 ± 0.52	5.95**	9.68***	3.82*
(n)	(15)	(14)	(15)	(14)	(15)	(17)			

We therefore suggest that differences in the sensitivity of these two species to natural variation in diet quality may contribute to indirect competition between *M. natalensis* and *M. coucha*. Similarly, Duplantier et al. ('96) argued that the wider distribution of *Mastomys erythroleucus*, compared to the restricted distribution of *Mastomys huberti* and *M. natalensis* in Senegal, could be explained by its greater reproductive performance, allowing it to colonize new habitats at higher rates. However, their study was conducted using only one dietary regime and did not consider the effect of food quality on differential reproductive rates. We therefore contend that the ability of

M. natalensis to differentially exploit areas of low resource availability within the more mesic part of southern Africa may give it a competitive advantage over *M. coucha* in such areas, thus contributing to interspecific competition between the two species. Correspondingly, Dickman ('86a,b) suggested that the intensity of interspecific competition between the small dasyurid marsupials, *Antechinus stuartii* and *A. swainsonii*, may be mediated through the relative abundance of these sympatric competitors. Experimental manipulation of the available resources, through supplementation of food quantity, has shown that resource limitation and interspecific competition

can play major roles in regulating rodent population density and structure (Brown and Munger, '85). Likewise, Koekemoer and van Aarde (2000) examined an African rodent community including *M. natalensis*. They demonstrated that an increase in food quantity reduced species diversity as a result of an increase in the abundance of *M. natalensis*. Clearly *M. natalensis* is capable of exploiting available resources more successfully than other rodents within the community.

Optimal dietary protein content differs between rodents. For example laboratory mice reproduce optimally on diets containing 17% protein (Knapka, '82), though considerable variation exists between strains. Laboratory rats, however, show maximal growth rates on diets containing 23% protein (Edozien and Switzer, '78), while white-footed mice *Peromyscus leucopus* select for foods containing 15% protein (Lewis et al., 2001). Field studies in Zimbabwe recorded *M. natalensis* with stomach contents whose protein content ranged from 22–30% (Swanepoel, '80), suggesting that protein levels in excess of 20% in their diet should not restrict breeding ability. In contrast, relatively high dietary protein levels may reduce the breeding effort of *M. coucha*. As we demonstrated, the age of sexual maturity is much greater, while female reproductive effort (litter:female mass ratio) is reduced on a 20% protein diet compared to individuals on a 15% protein diet. Numerous studies have indicated a critical upper limit of dietary protein levels for normal growth and maintenance (e.g. Edozien and Switzer, '78). However, given the ability of rodents to select for specific levels of protein in their diets (Musten et al., '74; Lewis et al., 2001) we would not necessarily expect this upper limit to be critical amongst free-ranging mice, as individuals would be able to select for dietary protein levels within their optimal limits. Thus, we predict that free-ranging female *M. coucha* should select a diet with a protein content of less than 20%, in order to maximise reproductive ability.

It is also not apparent why *M. coucha* litters produced by females on 20% dietary protein should exhibit a male-biased sex ratio (see also Lamb and van Aarde, 2001). Within the limitations of their food quality range, there was no variation in litter size, or the numbers of male pups with diet, suggesting that sex-specific foetal resorption or differential embryo mortality were not responsible (for house mice see Rivers and Crawford, '74; Krackow, '92; Meikle and Thornton, '95). The observed sex ratios are at odds with Trivers and Willards' ('73) theory of maternal sex ratio adjustment. This is partly because, while mothers on high protein diets produced more sons, those on low protein diets did not produce more daughters. Further, Trivers and Willard argue that the critical period for sex ratio adjustment is at the end of parental investment. If we consider this to be at weaning for *Mastomys*, and assume those pups in the best condition to be the heaviest, no significant differences were recorded in pup mass of mothers on 15– or 20% protein diets.

Mastomys natalensis mothers responded to low dietary protein by reducing litter size, but not pup mass, on diets containing less than 20% protein. However females on a 20% diet were significantly larger than females on other diets, such that the greater mass of their pups may in part have been a function of female size. Despite similarities in pup mass at birth, the mass of pups at weaning age increased with dietary protein. This suggests that while low dietary protein content may not have limited females' ability to control post partum pup mass, it did limit their ability to control weaning mass. This is perhaps not surprising given the increased energetic costs associated with lactation (Gittleman and Thompson, '88; Speakman et al., 2001), which are expected to increase with litter size (Smith and McManus, '75). Our results also showed a reduction in the percentage of mice that were weaned on a 6% protein diet.

Together, these results suggest that the quality of food available to females does not greatly effect their investment in individual pups at partum, though litter size is reduced on low quality diets. For a rodent with a high reproductive potential such as *M. natalensis*, this may be advantageous for several reasons, as it would allow females to conceive on lower quality diets than those necessary to maintain lactation. However, given the relative magnitude of differences in dry and wet season diet quality (crude protein content) in African savannah ecosystems (Mugangu et al., '95; Dörgeloh, '99), as well as the rapid improvement in vegetation quality at the start of wet periods (Owen-Smith, '94), the increase in the quality of food resources during gestation may be sufficient for females to successfully bear this extra energetic burden. If so it would allow females to wean offspring of comparable body mass to those born to mothers on higher quality diets. Thus, an ability to conceive on relatively poor diets would enable females to advance the date of conception, allowing them to respond more quickly to changes in food quality. Furthermore, it would allow females

to breed, albeit at a reduced rate, under conditions of sub-optimal food quality, such as within disturbed habitats.

The development of rodent plagues in tropical and sub-tropical regions is typically associated with years of high rainfall (Leirs et al., '96, Lima et al., '99; Singleton et al., 2001). More critically, plagues may predictably develop in years experiencing early rains, leading to extended breeding periods. This is important in allowing populations to breed up to pest proportions (Leirs et al., '96), while Singleton et al. (2001) also suggest it is important for plague events that females can initiate reproduction at small body size. Our results suggest an additional factor contributing to an advancement of the onset of seasonal breeding may be the ability of so-called pest species to initiate breeding earlier, using lower quality diets than non-pest species, even if diet quality is insufficient at the time to maintain more optimal lactational rates of energy and protein intake. In such circumstances an improvement in food quality per se may not be necessary to trigger breeding activity, but to allow females to successfully rear early litters.

ACKNOWLEDGEMENTS

LITERATURE CITED

Avenant NL. 1997. Mammals recorded in the QwaQwa National Park (1994–1995). Koedoe 40:31–40.

Avenant NL. 2000. Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. S Afr J Wildl Res 30:26–33.

Bomford M. 1987a. Food and reproduction of wild house mice. 1. Diet and breeding seasons in various habitats on irrigated cereal farms in New South Wales. Aust Wildlife Res 125:183–196.

Bomford M. 1987b. Food and reproduction of wild house mice. 3. Experiments on the breeding performance of caged house mice fed rice-based diets. Aust Wildlife Res 14:207–218.

Bomford M, Redhead T. 1987. A field experiment to examine the effects of food quality and population density on reproduction of wild house mice. Oikos 48:304–311.

Boutin S. 1990. Food supplementation experiments with terrestrial vertebrates:patterns, problems, and the future. Can J Zool 68:203–220.

Bowland AE, Perrin MR. 1988. The effect of fire on the small mammal community in Hluhluwe Game Reserve. Z Saugetierkd 53:235–244.

Brown JH, Munger JC. 1985. Experimental manipulation of a desert rodent community:food addition and species removal. Ecology 66:1545–1563.

Cameron GN, Eshelman BD. 1996. Growth and reproduction of hispid cotton rats (*Sigmodon hispidus*) in response to naturally occurring levels of dietary protein. J Mammal 77:220–231.

Chidumayo EN. 1980. Ecology of rodents at an old quarry in Zambia. S Afr J Zool 15:44–49.

Chidumayo EN. 1984. Observations on populations of multimammate mice at Livingstone, Zambia. Mammalia 48: 363–376.

Christensen JT. 1993. The seasonal variation in breeding and growth of *Mastomys natalensis* (Rodentia, Muridae):evidence for resource limitation. Afr J Ecol 31:1–9.

Christensen JT. 1996. Home range and abundance of *Mastomys natalensis* (Smith, 1834) in habitats affected by cultivation. Afr J Ecol 34:298–311.

DeLong KT. 1967. Population ecology of feral house mice. Ecology 48:611–634.

Dickman CR. 1986a. An experimental study of competition between two species of dasyurid marsupials. Ecol Monogr 56:221–241.

Dickman CR. 1986b. An experimental manipulation of the intensity of interspecific competition:effects on a small marsupial. Oecologia 70:536–543.

Dippenaar NJ, Swanepoel P, Gordon DH. 1993. Diagnostic morphometrics of two medically important southern African rodents, *Mastomys natalensis* and *Mastomys coucha* (Rodentia, Muridae). S Afr J Sci 89:300–303.

Dörgeloh WG. 1999. Chemical quality of the burnt and non-burnt grass layer in the Nylsvlei Nature Reserve, South Africa. Afr J Ecol 37:168–179.

Duplantier JM, Granjon L, Bouganaly H. 1996. Reproductive characteristics of three sympatric species of *Mastomys* in Senegal, as observed in the field and in captivity. Mammalia 60:629–638.

Edozien JC, Switzer BR. 1978. Influence of diet on growth in the rat. J Nutr 108:282–290.

Ferreira SM, van Aarde RJ. 1996. Changes in community characteristics of small mammals in rehabilitating coastal dune forests in northern Kwazulu/Natal. Afr J Ecol 34: 113–130.

Fiedler LA. 1988a. Rodent problems in Africa. In:Prakash I, editor. Rodent Pest Management. Boca Raton, FL:CRC Press. p 35–65.

Fiedler LA. 1988 b. Rodent pest problems and management in eastern Africa. FAO Plant Protect. B. 36:125–134.

Field AC. 1975. Seasonal changes in reproduction, diet and body composition of two equatorial rodents. E Afr Wildl J 13:221–235.

Firquet E, Leirs, H, Bronner, G. 1996. Germinating grasses and reproductive seasonality of *Mastomys* species (Rodentia, Muridae). Mammalia 60:775–779.

Ford RG, Pitelka FA. 1984. Resource limitation in populations of the California vole. Ecology 65:122–136.

Gittleman JL, Thompson SD 1988. Energy allocation in mammalian reproduction. Am Zool 28:863–875.

Gordon DH. 1984. Evolutionary genetics of the *Praomys* (*Mastomys*) natalensis species complex (Rodentia:Muridae). PhD thesis, University of the Witwatersrand.

Granjon L, Duplantier JM, Catalan J, Britton-Davidian J. 1997. Systematics of the genus *Mastomys* (Thomas, 1915) (Rodentia, Muridae):a review. Belg J Zool 127:7–18.

Green CA, Gordon DH, Lyons NF. 1978. Biological species in *Praomys* (*Mastomys*) *natalensis*, a rodent carrier of Lassa virus and bubonic plague in Africa. Am J Trop Med Hyg 27:627–629.

Hansen TF, Stenseth NC, Henttonen, H. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density-dependence. Am Nat 154:129–139.

Hoffmann RS. 1958. The role of reproduction and mortality in population fluctuations of voles (*Microtus*). Ecol. Monogr. 28:79–109.

Ims RA. 1987. Differential reproductive success in a peak population of the greysided vole *Clethr ionomys rufocanus*. Oikos 50:103–113.

Johnston HL, Oliff WD. 1954. The oestrous cycle of female *Rattus* (*Mastomys*) *natalensis* (Smith) as observed in the laboratory. P Zool Soc Lond 124:605–613.

Karels TJ, Boonstra R. 2000. Concurrent density-dependence and independence in populations of arctic ground squirrels. Nature 408:460–463.

Knapka JJ. 1982. Nutrition. In:Foster HL, Small JD, Fox JG, editors. The mouse in biomedical research. Volume 3. New York:Academic Press. p 52–67.

Koekemoer AC, van Aarde RJ. 2000. The influence of food supplementation on a coastal dune rodent community. Afr J Ecol 38:343–351.

Krackow S. 1992. Sex ratio manipulation in wild house mice:the effect of fetal resorption in relation to the mode of reproduction. Biol Reprod 47:541–548.

Krebs CJ. 1999. Current paradigms of rodent population dynamics:what are we missing? In:Singleton GR, Hinds LA, Leirs H, Zhang Z, editors. Ecologically-based rodent management. Canberra:Australian Centre for International Agricultural Research Monograph 59. p 33–48.

Krebs CJ and DeLong KT. 1965. A *Microtus* population with supplemental food. J Mammal 46:566–573.

Lamb CE and van Aarde RJ. 2001. Maternal dietary protein intake and sex-specific investment in Mastomys coucha (Rodentia:Muridae). J Zool Lond 253:505–512.

Leirs H, Stuyck J, Verhagen R, Verheyen, W. 1990. Seasonal variation in growth of *Mastomys natalensis* (Rodentia, Muridae) in Morogoro, Tanzania. Afr J Ecol 28: 298–306.

Leirs H, Verhagen R, Verheyen W. 1993. Productivity of different generations in a population of *Mastomys natalensis* rats in Tanzania. Oikos 68:53–60.

Leirs H, Verhagen R, Verheyen W. 1994. The basis of reproductive seasonality in *Mastomys* rats (Rodentia:Muridae) in Tanzania. J. Trop. Ecol. 10:55–66.

Leirs H, Verhagen R, Verheyen W, Mwanjabe P, Mbise T. 1996. Forecasting rodent outbreaks in Africa:an ecological basis for *Mastomys* control in Tanzania. J Appl Ecol 33: 937–943.

Leirs H, Stenseth NC, Nichols JD, Hines JE, Verhagen R, Verheyen W. 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. Nature 389:176–180.

Lewellen RH, Vessey SH. 1998a. Modelling biotic and abiotic influences on population size in small mammals. Oecologia 113:210–218.

Lewellen RH, Vessey SH. 1998b. The Effect of density dependence and weather on population size of a polyvoltine species. Ecol Monogr 68:571–594.

Lewis CE, Clark TW, Derting TL. 2001. Food selection by the white-footed mouse (*Peromyscus leucopus*) on the basis of energy and protein contents. Can J Zool 79:562–568.

Lima M, Keymer JE, Jaksic FM. 1999. El Nino southern oscillation driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America:linking demography and population dynamics. Am Nat 153:476–491.

Meester J. 1960. Early post-natal development of multimammate mice *Rattus* (*Mastomys*) *natalensis* (A. Smith). Ann Transvaal Mus 24:35–52.

Meester JAJ, Lloyd CNV, Rowe-Rowe DT. 1979. A note on the ecological role of *Praomys natalensis*. S Afr J Sci 75: 183–184.

Meikle DB, Thornton MW. 1995. Premating and gestational effects of maternal nutrition on secondary sex ratio in mice. J Reprod Fertil 105:193–196.

Monadjem A. 1998. Reproductive biology, age structure, and diet of *Mastomys natalensis* (Muridae, Rodentia) in a Swaziland grassland. Z Saugetierkd 63:347–356.

Monadjem A, Perrin MR. 1996. The effects of additional food on the demography of rodents in a subtropical grassland in Swaziland. Mammalia 60:785–789.

Mugangu TE, Hunter ML, Gilbert JR 1995. Food, water, and predation:a study of habitat selection by buffalo in Virunga National Park, Zaire. Mammalia 59:349–362.

Musten B, Peace D, Anderson GH. 1974. Food intake regulation in the weanling rat:self-selection of protein and energy. J Nutr 104:563–573.

Owen-Smith N. 1994. Foraging responses of kudus to seasonal changes in food resources:elasticity in constraints. Ecology 75:1050–1062.

Perrin MR, Clarke JR. 1987. A preliminary investigation of the bioenergetics of pregnancy and lactation of *Praomys natalensis* and *Saccostomus campestris*. S Afr J Zool 22: 77–82.

Rivers JPW, Crawford MA. 1974. Maternal nutrition and the sex ratio at birth. Nature 252:297–298.

Saitoh T, Bjornstad ON, Stenseth NC. 1999. Density-dependence in voles and mice:a comparative study. Ecology 80:638–650.

Singleton G, Krebs CJ, Davis S, Chambers L, Brown P. 2001. Reproductive changes in fluctuating house mouse populations in South-Eastern Australia. Proc Roy Soc Lond B 268:1741–1748.

Smit A, Vanderbank H, Falk T, Decastro A. 2001. Biochemical genetic markers to identify two morphologically similar South African *Mastomys* species (Rodentia, Muridae). Biochem Syst Ecol 29:21–30.

Smith BW, McManus JJ. 1975. The effects of litter size on the bioenergetics and water requirements of lactating Mus musculus. Comp Biochem Physiol 51A:111–115.

Sokal RR, Rohlf FJ. 1995. Biometry:the principles and practice of statistics in biological research. New York:W.H. Freeman.

Speakman JR, Gidney A, Bett J, Mitchell IP, Johnson MS. 2001. Limits to sustained energy intake IV. Effect of

variation in food quality on lactating mice *Mus musculus*. J Exp Biol 204:1957–1965.

Statsoft, Inc. 1996. Statistica for windows. Tulsa, Oklahoma

Stenseth NC, Leirs H, Mercelis S, Mwanjabe P. 2001. Comparing strategies for controlling an African pest rodent:an empirically based theoretical study. J Appl Ecol 38:1020–1031.

Swanepoel CM. 1980. Some factors influencing the breeding season of *Praomys natalensis*. S Afr J Zool 15: 95–98.

Swanepoel CM. 1981. The effect of fire on a small mammal community. S Afr J Zool 16:232–236.

Taylor KD, Green MG. 1976. The influence of rainfall on diet and reproduction in four African rodent species. J Zool Lond 180:367–389.

Tkadlec E, Zejda J. 1998. Density-dependent life histories in female bank voles from fluctuating populations. J Anim Ecol 67:863–873.

Trivers RL, Willard DE. 1973. Natural selection of parental ability to vary sex ratio of offspring. Science 179:90–92.